Mem. Qd Mus. **21**(2): 361—85. [1984]

AN INTERPRETATION OF THE STRUCTURE AND FUNCTION OF THE ANTENNAL SENSE ORGANS OF *MELITTOBIA AUSTRALICA* (HYMENOPTERA : EULOPHIDAE) WITH THE DISCOVERY OF A LARGE DERMAL GLAND IN THE MALE SCAPE.

EDWARD C. DAHMS
Queensland Museum

ABSTRACT

The importance of the antennae during courtship behaviour of *Melittobia* species prompted an investigation into the histology of the enlarged male scape using the single Australian species *Melittobia australica*. The application of the male scape during courtship suggests a possible chemical communication between the antennae of the two sexes. Histological and SEM work reveal the presence of a large dermal gland in the male scape. SEM work and chemical applications reveal the presence of long thin unfluted setae, tapering fluted setae, multiporous plate sensilla and short basiconic capitate pegs on the antennae of both sexes (the short basiconic capitate pegs are absent in most males). Together with behavioural observations these are used to suggest the possible structure and function of the antennal sense organs and the most likely receptor for the male scape pheromone.

MALE SCAPE

Amongst the parasitic Hymenoptera, male antennation is a common component of precopulatory behaviour and it reaches a high expression in *Melittobia* (Gordh and DeBach (1978)). The enlargement of the male scape and its application discussed by Dahms (1983b) suggest that it has a function in stimulating the female's antennae. In males of all species cleared in 10% NaOH the scapes show a clear delimited zone (Pl. 1a, *M. australica*). In *M. australica* the surface appears to have a cellular pattern at higher magnifications. Since all internal tissue is removed in this process, the clear delimited zones must be cuticular which suggests mechanical stimulation of the female's flagellum. However, freshly killed *M. australica* males used for $AgNO_3$ staining to test for touch chemoreceptors when examined after 30 minutes in Toluene were found to be not completely cleared. In the scapes of these males could be seen a cellular-like zone occupying the same area as the clear delimited zone in NaOH cleared specimens. (Pl. 1a) is a lateral view of the side opposite pedicel attachment and (Pl. 1b) is an end view of the same side. This cellular-like zone was absent in specimens fully cleared in Toluene indicating that it was internal tissue. Serial sectioning of male *M. australica* scapes clearly shows large dermal glands which follow the clear delimited zone in NaOH cleared specimens (Pl. 3b, c; 4a). The sections also show that the inner cuticular lining on the scape groove is much thinner than the outer cuticle and that there are cuticular infoldings along the length of the gland. These cuticular infoldings form the limits of the clear zone in NaOH cleared specimens.

To prepare them for SEM examination, males were treated with 10% NaOH until cleared to remove any glandular secretions which might obscure the cuticular surface of the gland. They were then dehydrated in alcohol and finally treated with Toluene to remove any wax which might obscure cuticular pores. Males were air dried and mounted upside down on stubs in preparation for gold coating. It was noticed that after removal from Toluene and air drying the flexible intersegmental cuticular areas became white while the thicker cuticular sclerites remained yellow-brown. The lining of the scape groove became white indicating that it was flexible thin cuticle, which would explain the cuticular infoldings around the gland for support. SEM photomicrographs (Pl. 2b, c; 3a) show the cuticular surface over the gland to be well differentiated and perforated by numerous pores. At higher magnifications the cuticular surface over the gland shows a somewhat reticulate

appearance. Noirot and Queenedey (1974) mention cuticular specialisations in Heteroptera, Blattodea and butterflies associated with dermal glands and that these serve as evaporative areas ensuring rapid evaporation of secretions. The cuticular area over the scape gland in *M. australica* fits this pattern.

The shape, size and position of the scape gland varies with species and provides a very useful taxonomic tool. I refer the reader to my taxonomic revision of the genus (Dahms 1983a) for a fuller discussion together with figures and a discussion of species groups.

Van den Assem et alia (1982: 458) raise a rather interesting point. They found that males with their antennae removed do court females and induce receptivity. From this they concluded that stimuli which might arise from them are by no means necessary. The data they present are from mutilation experiments with *M. acasta* (Walker) and it is not clear from their account if they carried out similar trials with all species at their disposal. If we look at the male scape gland in *M. acasta* it is not as extensive as in the *hawaiiensis* and *assemi* groups. The cuticle over the scape gland in *M. acasta* as shown by Van den Assem et alia (1982, Pl. 1) does not appear to have an evaporative function as it does in *M. australica* (Pl. 2c, 3a). Perhaps the scape gland does not have the importance in the *acasta* group that it has in the *hawaiiensis* and *assemi* groups. It is interesting to note also that antennal contact is permanent throughout courtship in the *hawaiiensis* and *assemi* groups but only through part of the cycle in *M. acasta* and *M. evansi* Dahms (1983a) but not in *M. digitata* Dahms (1983a). There may be some variation in the importance of permanent antennal contact in some members of the *acasta* group (not studied by Van den Assem et alia (1982)) which seem to have relatively expanded scape glands eg. *M. femorata* Dahms (1983a) and *M. chabylii* Ashmead. In the latter the scape gland in genicualte as in the *hawaiiensis* and *assemi* groups although that of *M. chabylii* is not as extensive.

Goodpasture (1975) observed pores in the modified scapes of the torymid chalcidoid wasps *Monodontomerus montivagus* Ashmead and *M. clementi* Grissell which were applied to the tip of the female flagellum during the climax phase of courtship. He concluded that the male scapes might be the source of chemical communication as a behavioural cue and further suggested that the pores indicated either a chemical sensory function or pheromone elaboration sites. From my studies on *M. australica* I suggest that they are probably the latter. Antennation during courtship is a common phenomenon in Chalcidoidea and is often accompanied by antennal modifications. Pheromone glands in male antennae may also be a common occurrence. Houston (1975) has found antennal modifications containing dermal glands in several Australian species of the bee genus *Hylaeus*. Antennal modifications containing glands may be more widespread in the Hymenoptera than current knowledge indicates.

ANTENNAL SENSE ORGANS

During the course of a biological study on *M. australica* Dahms (1983b) it was decided to investigate the sense organs on the antennae since the latter play an important part in precopulatory behaviour. The following discussion is based on SEM work, behavioural observations and a few chemical applications. It does not have the benefit of histological or electro-physiological data, therefore the structures and functions of the sense organs are suggested rather than conclusively proven.

Males of all species of *Melittobia* have their compound eyes reduced to a single ocellus-like spot. Picard (1922) examined *M. acasta* males histologically and found that the reduced eyes lacked the normal structural elements of even an ocellus. The optic ganglia were also reduced relative to the female. He related this reduction, together with shortened wings and relatively reduced pigmentation, to the male's restriction to the host cell or puparium in which they emerge. This reduction in functional elements in the eyes of males is no doubt general in the genus.

The sole function of the male is related to reproduction. Van den Assem and Putters (1980) found that sound production is not involved in the courtship of *Melittobia*. Presumably males rely on chemical and tactile stimuli for locating females and for precopulatory behaviour. Chemical information appears to play an important role in the behaviour of both sexes. The size of the complex gland in the male scape and the role of this segment during precopulatory behaviour suggests that the female receives a considerable chemical input during antennation. Behavioural observations (mentioned under 'Long thin unfluted setae' below) indicate that the sexes are chemically different and there are easily discernible behaviour patterns depending on the sex encountered by individuals of both sexes. Females have additional occasions in which olfactory reception could be important e.g. host

location and feeding. The antennae of both sexes have setae whose structure suggests tactile receptivity.

SEM examination of the antennae of males and females of *M. australica* revealed the presence of the following sensory structures:-

1) long thin unfluted setae
2) tapering fluted setae
3) multiporous plate sensilla
4) short basiconic capitate pegs

1) Long thin unfluted setae (Pl. 5b,)

These are readily distinguished by the absence of both a basal socket and fluting. They are only present on the club of both sexes especially at the tip of the terminal segment.

Lack of a socketed base suggests they are not tactile in function. A possible contact chemoreceptive function is suggested by their concentration at the tips of the antennae, particularly noticeable in males, and by behavioural observations.

A male can instantly distinguish between the sexes by tapping another individual with the tips of his antennae. His behaviour varies dramatically according to the sex encountered; another male induces aggression, a female is mounted.

Females can also distinguish between the sexes. Virgin female *M. australica* when confined without males stand around with their mandibles open. When provided with a dead male pupa they immediately become active and begin searching behaviour. When another female is encountered they stop, palpate the encountered female with the tips of the antennae then resume searching behaviour. When the dead male pupa was encountered and palpated, searching behaviour ceased. The females stood around the pupa continually palpating it with the tips of their antennae. Some of the females opened their mandibles. In cultures, similar reactions occurred and it was not uncommon to see groups of females standing around a male engaged in courtship, palpating him with the tips of their antennae. Mandibular opening was also observed in these groups of virgin females and it suggests that mandibular glands could be the source of a female odour. Gordh and DeBach (1978) mentioned that mandibular involvement in courtship appears to be an adaptation in some Chalcidoidea; also studies showed that olfaction could be used for mate attraction. They suggested that the gland-like ducts in the mandibles of chalcidoids may indicate exocrine glands. The mandibles of both sexes in *Melittobia* have two such gland-like ducts. During courtship in *M. australica,* mandibular opening by females occurs towards the end of the sequence which brings them into close proximity with the flagellum of the male.

Female behaviour on a host also suggests a contact chemoreceptive function for thse sensilla. A fertilised female uses her ovipositor to puncture the host then feeds on the droplet of host body fluid that wells forth. After withdrawal of the ovipositor the female moves backwards palpating the surface of the host with the tips of her antennae until the droplet is encountered. At this point feeding begins. Female *M. australica* revisit old puncture sites to feed upon congealed host body fluids which they relocate by palpation with the tips of their antennae.

SEM examination of the tip of these setae does not reveal the typical pores of contact chemoreceptor sensillae. Following the procedures of Slifer, Prestage and Beams (1957) very good results were obtained using $AgNo_3$. After 60 minutes, the $AgNo_3$ had penetrated the tips of these setae (Pl. 5a). The penetration was more rapid in males than in females which is probably related to the setae being of larger diameter in the males. These tests, behavioural observations and location of these setae suggest therefore that they are touch chemoreceptors.

In the female, touch chemoreceptors on the terminal antennal segments would also be of use in host identification. Female *M. australica* walk over a host nest palpating it with their antennae. Once it has been identified and entered these sensillae may be of use in detecting the presence of enveloping membranes, e.g. cocoons. They may also help differentiate hosts e.g. oviposition behaviour differs between hymenopteran and some dipteran hosts. Should a *Melittobia* female enter a host cell when the host is immature these sensillae would allow her to distinguish between the host and its provisioned food. The relative amount of food provision and its state of preservation may be of use in distinguishing if the host had failed or its stage of development. On the other hand these sensillae may be used directly to ascertain the age of the host. No information is available on whether there are chemical differences between the different stages of a host, but since the hymenopteran hosts I have observed accumulate waste internally and pass it out just before pupation as meconium, the relative amount of internally accumulated waste or the presence of meconium may be an important sensory signal for oviposition in *Melittobia.*

Finally these sensilla may be useful in detecting the suitability of a host i.e. whether the host is diseased.

2) Tapering fluted setae (Pl. 5b, ii)

These arise from a socketed base and show a slightly whorled fluting on the surface (Pl. 6d). They do not take up $AgNO_3$ stain. The fluting provides rigidity allowing the setae to resist bending thus transferring maximum movement to the socketed bases. In the male they are present on all antennal segments with marked differentiation. On the proximal segments of the flagellum they are long and numerous, but are reduced in length and number towards the terminal club segment (Pl. 6a). On the other segments of the antenna they are also relatively shorter and are fairly evenly distributed except for their absence on the lining of the scape groove and for a relatively denser arrangement of shortish setae on the upper surface of the lateral expansion of the pedicel. In the female they are present on all segments of the antenna and have a fairly even distribution (slightly fewer on the club) without any size differentiation. In general, they are shorter and finer than in the male and they are shorter and finer than the long thick non-fluted setae on the clubs of both sexes.

Because of the fluting and socketed base I assume they are touch receptors. Their general uniformity in size and shape in the female indicates they have no specific function, just providing generalised tactile information, e.g. they would be of assistance in estimating the size of the hole the female excavates in the host cell. In this way the female would be able to estimate if the excavation is wide enough and when penetration has been effected. Female *M. australica* when excavating in a *Sceliphron formosum* nest were noted to insert their antennae periodically and touch the walls of the excavation with the sides of the flagellum. Differentiation of these sensilla on the male flagellum suggests a specific function. When a male encounters a female he mounts her first then searches for her head with his antennae. When he mounts a female he orientates longitudinally on her and taps his flagella either side of the female's extremity like a pair of cupped hands thus engaging the long setae on the proximal flagellar segments. When the female's posterior metasoma is touched the male turns 180° and repeats the procedure at the head then scoops her antennae into his scape groove. Where the female's head is touched no turning occurs. This may not be the only sensory input e.g. if the female produces a female scent from mandibular glands then orientation on the female could also involve olfactory information via his multiporous plate sensilla.

Before passing on to the other sensilla, mention should be made of two clusters of differentiated, socketed, fluted setae occuring on leg segments in the male. In *M. australica* and *M. hawaiiensis* males the ventral surfaces of the fore-trochanters bear a dense tuft of thick, short, socketed setae with whorled fluting (Pl. 4b). In males of all other known species except *M. chalybii* where they are not as well developed the fore-trochanters have a few fine, undifferentiated, scattered setae ventrally. During courtship of *M. australica* and *M. hawaiiensis* these setae press firmly down on the pronotum of the female. In all other species for which courtship is known, the position of the male is such that the fore trochanters are not in contact with the female. It is difficult to suggest the use that these serve, but since modifications in male *Melittobia* morphology are closely linked to some aspect of courtship there must be some important sensory input via these setae. Perhaps they are useful in positioning the male for courtship.

Another group of differentiated, fluted setae with socketed bases occur on the posterior ventral surfaces of the mid femora of males of all species and ventrally on the mid trochanters of all species except *M. australica* and *M. hawaiiensis*. Those of *M. australica* are definitely socketed with shallow, unwhorled fluting (Pl. 4c). These setae in all species are much longer than the general body setation and there is some differentiation amongst them. The mid legs are used by the males of all species during courtship and in *M. australica* these setae were noted to brush the 'shoulder' junction of the pro- and mesonotum of the female. The pattern of distribution and the degree of differentiation amongst these setae varies with the species Dahms (1983a). It would be interesting to see if these variations are related to specific differences in male mid leg movements and/or the parts of the females brushed. Their function in the male may be to signal contact with that part of the female to be stroked and their input to the female would most likely be tactile also via her undifferentiated general body setation. Females do show differentiated long setae on the posterior pronotum, the mid-lobe of the mesoscutum and the scutellum, but these are not in a position to be stimulated by the differentiated mid leg setae of the male.

3) Multiporous plate sensilla (plate organs) (Pl. 5b, iii).

These are raised sensilla which appear as pale areas on dry and slide-mounted antennae of most Hymenoptera. In *Melittobia* they are elongate (0.009 × 0.003 mm) on female club segments of *M. australica*) and are present on all flagellar segments in both sexes except for males of the *M. hawaiiensis* and *M. assemi* groups where they are restricted to the club segments only. On the funicle segments they tend to be orientated transversely and in general they are fewer in number than on the middle club segment. On the club segments they tend to be longitudinal in arrangement and the transverse arrangement on the funicle segments may be related to the smaller number per segment. Distribution on each segment is uniform, i.e. there is no accumulation on any one side. The pattern of distribution along the antenna seems to vary with species and there is a small amount of intraspecific variation.

Multiporous plate sensillae have been assigned various functions, e.g. mechanoreceptors (Merlin 1941), auditory receptors (Ruland, 1888), air pressure receptors (McIndoo 1914, 1922), photoreceptors (Booth, 1963) and so on. More recent work indicates an olfactory function. The reaction of *M. australica* multiporous plate sensilla to ethyl acetate (discussed later) certainly indicates a reaction to chemicals.

Studies by Slifer, Prestage and Beams (1959) showed that some of the peg sensilla on the flagellum of grasshoppers had numerous fine pores in their cuticular walls and these could be demonstrated by soaking the antenna in 0.5% methylene blue. Sections revealed fine nerve fibres running to each pore. Further work has shown these to be olfactory receptors. Electrophysiological work by Lacher and Schneider (1963) and Lacher (1964) has shown that the multiporous plate sensilla on honey bee (*Apis mellifera*) antennae are olfactory. Slifer and Sekhon (1961) demonstrated fine pores in the cuticle of these, but not the fine fibrils. Slifer (1969) felt that further examination will probably reveal fine fibrils passing to these pores. Multiporous plate sensilla in aphids examined by Slifer, Sekhon and Lees (1964) differ in structure from those of the honey bee partly in the possession of an inner and outer cuticular layer. Dedrites pass singly or in groups through pores in the inner cuticular layer and enter a fluid filled chamber between the two cuticular layers in which they branch repeatedly. The fluid filled chamber has some importance in interpreting results obtained when I treated *M. australica* females with ethyl acetate (discussed later). The outer cuticular layer of aphid multiporous plate sensilla are penetrated by numerous fine pores each supplied with fine fibrils. It could not be determined if these fine fibrils were connected to the dendrites, but Slifer, Sekhon and Lees (1964) felt this was probably the case. Freshly moulted specimens admitted crystal violet dye through these pores. The presence of fine filaments terminating in the pores plus the staining via these pores were taken to indicate an olfactory function for aphid multiporous plate sensilla.

Slifer (1969) examined the sense organs on the antennae of the pteromalid wasp *Nasonia vitripennis* (Walker). When treated with 0.5% crystal violet dye the stain rapidly entered the multiporous plate sensillum and examination showed the presence of numerous fine pores in the surface. In cross section these multiporous plate sensilla were seen to have an inner membrane similar to the multiporous plate sensilla of aphids. The inner cuticle lies just above two shelf-like invaginations of the cuticle. She noticed a large group of dendrites just below the proximal end of the inner membrane and presumed that these passed through the inner membrane, as in the aphid, and sent filaments into the pores in the outer surface.

The multiporous plate sensilla of *M. australica* resemble those of *Nasonia vitripennis* in overall shape and appearance. In cleared specimens, two longitudinal cuticular invaginations can be seen on either side of the multiporous plate sensilla as in *N. vitripennis*. I have not carried out histological investigation of the *M. australica* multiporous plate sensilla to confirm the presence of an inner membrane but am fairly certain there is one. Attempts to demonstrate pores in the outer wall using 0.5% crystal violet solution as used by Slifer (1960, 1969) were not successful even in freshly moulted specimens and SEM investigations did not reveal pores either. Slifer, Sekhon and Lees (1964) found that the plate organs of aphids showed crystal violet penetration when fixed four hours after the final moult but no penetration at 24 hours and 48 hours after final moult. They suggested that the minute pores in the older specimens might be rimmed with a waxy or hydrophobic material which prevents entry of the dye. Locke (1964) when discussing the formation of the insect cuticle states that the secretion of the endocuticle and the secretion of wax can occur concurrently and extend through the intermoult period. Therefore, it is possible that wax secretions constrict the pores after moulting. Pl. 8a–c show

the thin walled basiconic pegs of the grasshoppers *Atractomorpha similis* (Bolivar) freshly moulted and *Valanga irregularis* (Walker) several hours after moulting. The difference between the two is thought to be a result of wax encroachment. Gold coating would further fill the fine pores and obscure them in older specimens.

The normal method used for preparing *M. australica* for SEM examination involved killing by immersion in 75% ethyl alcohol before gold coating. When freshly moulted specimens were killed using ethyl acetate vapour before gold coating the result showed multiporous plate sensilla with a crumb-like surface which at higher magnifications look like exudations from pores in the surface (Pl. 6b–d). It can be seen that the surface of the antenna lacks the usual crazed appearance of older antennae and this is thought to be because the wax layer was absent or very thin. Older specimens when killed with ethyl acetate showed multiporous plate sensilla with a blistered appearance and distribution of the blisters matched distribution of the exudations in freshly moulted specimens (Pl. 6d). It is thought that the exudations arise from the fluid filled space between the outer and inner membranes of the multiporous plate sensilla and that this is in response to fairly high ethyl acetate concentration being an attempt to protect the sensitive nerve ending from a pungent vapour. The analogy is to the mammalian nasal mucosa which produces copious mucus in response to pungent vapours.

Barlin and Vinson (1981) investigated the multiporous plate sensilla on the antennae of several species of Chalcidoidea. In some cases they also found that the presence of pores in the outer plate was shown by exudations. Their investigations revealed two types of multiporous plate sensilla; Type 1 – present in both sexes and possessing a thin outer cuticle with numerous pores; Type 2 – present in females only and possessing a thick outer cuticle with fewer pores. Both types were found in all species studied except three i.e. not all species were found to have Type 2 multiporous plate sensilla. In *M. australica,* the females appear to have only Type 1. However, my work on *M. australica* antennal sense organs was carried out some time before the appearance of the paper by Barlin and Vinson and time does not permit a more thorough investigation of this aspect. I have not investigated the multiporous plate sensilla on the male antennae.

The similarity of the multiporous plate sensillae of *M. australica* to those of *Nasonia vitripennis,* the presence of pores on the outer surface in conjunction with the results of Slifer et alia on other receptors having porous surfaces and the results of Barlin and Vinson with various chalcidoids suggest strongly that the multiporous plate sensilla of *M. australica* are olfactory in function. From their reaction to ethyl acetate they are probably very sensitive.

Before discussing their function we should look at the short basiconic capitate pegs as these appear also to be olfactory in function.

4) Short basiconic capitate pegs (Pl. 5b, iv).

These organs are absent from the antennae of males of most species but are present on the funicle and club of females where they predominate on the dorsal or outer surface. They arise from a circular, shallow, relatively broad depression in the cuticle. Thereafter the peg tapers into stalk which terminates in a spherical knob, the whole resembling a champagne cork. They occur sub-marginally on the distal portions of the segments and are directed towards the distal tip of the antenna.

These were not recorded on the antennae of *Nasonia vitripennis* by Slifer (1969) but were found subsequently in this species and another pteromalid wasp *Peridesmia discus* (Walker) by Miller (1972). Weseloh (1972) found them on the antennae of the encyrtid wasp *Cheiloneurus noxius* Compere. Neither gave any details of their ultrastructure but Miller (1972) assumed they were not touch receptors because of their sheltered location. Slifer, Prestage and Beams (1957,1959) suggest that basiconic capitate pegs may function in olfaction if they are thin walled or in the perception of irritant substances if they are thick walled.

When females of *M. australica* were killed by immersion in 75% ethyl alcohol, SEM examination showed no details other than a crazed surface thought to be wax (Pl. 7a). Freshly moulted females killed with ethyl acetate vapours showed weeping from slits or rows of pores arranged along the longitudinal axis of its capitate tip or caput. In Pl. 7b–d these slits or rows of pores can be seen quite clearly. The distal tip of the caput was devoid of exudations and resembled a tonsure. Around the base of the peg were exudations resembling those of the multiporous plate sensilla.

If one is to accept the reasoning put forward earlier to explain the exudations from multiporous plate sensillae then the internal structure and the function of the short basiconic capitate pegs may be the same as the multiporous plate sensilla. They are undoubtedly olfactory in function. Therefore there are two

morphologically different olfactory sensilla on the antennae of all females and some males.

Schneider and Steinbrecht (1968) when discussing insect olfactory sensilla indicated there are two physiological types of olfactory cells — odour specialists and odour generalists. The former respond to biologically important odours, e.g. sex attractants, warning or specific food odours. Both types may be found in the one sensillum and this has been demonstrated in the multiporous sensilla of the honey bee *Apis mellifera.*

In *Melittobia,* evidence suggests specific and sexually different chemical signals. The sources are the male scape gland and circumstantial evidence indicates mandibular glands in both sexes. These would suggest the presence of odour specialist, olfactory cells. Electro-physiological work would be required to identify the presence and location of these cells but some speculation is possible.

In the males of most species the antennae lack short basiconic capitate pegs. In females these are located mostly on the upper surface of the antennae which is the surface applied to the inner lining of the male scape groove or cup containing the dermal gland. The short basiconic capitate pegs therefore might contain odour specialist olfactory cells for perception of a male pheromone. Females are able to detect males from a distance, e.g. when a male is placed in with a group of inactive virgin females the latter immediately become active and move fairly directly towards the male. Hermann (1971) mentions male calling in *M. chalybii* (= *M. australica*). It was noticed in my colonies of *M. australica* that males walk about with their scapes raised laterally and flagellar segments extended so that the tip of the scape groove was open. They also stand around in this pose. It could be that they are exposing their scape gland to attract females. The rearing jars are much larger than the host cell or puparium and it is difficult to imagine the need for such a system in the confines of a host cocoon or puparium.

The distribution of multiporous plate sensilla varies in males. In the *hawaiiensis* and *assemi* groups they occur on the club segments only, but in the *acasta* group they occur on all flagellar segments. During courtship *M. australica* females were noticed to open their mandibles. Initially I thought this to be the signal for the female's readiness to copulate thus inducing the male's finale. However, van den Assem does not agree (Pers. comm. 1980). Mention has been made previously of virgin females without males standing with open mandibles. When provided with a dead male pupa females located it and again stood with open mandibles. It was argued that mandibular glands may be the source of female scent and if this is so then opening mandibles during courtship probably means some chemical input by the female. If virgin females call by mandibular glands then the only olfactory receptors in most males are the plate organs and these would contain the odour specialist olfactory cells. During courtship of species in the *hawaiiensis* and *assemi* groups the male position is such that his clubs are in close proximity to the female's mandibles when open. In these groups only male club segments bear plate organs. During courtship of the *acasta* group the male does not stand so far forward and his funicular segments would be in contact with her open mandibles. This is thought to have some bearing on retention of plate organs on the funicle as well as the club segments in the *acasta* group males.

ACKNOWLEDGMENTS

This paper is taken from my M.Sc. thesis submitted to the University of Queensland in 1982. My superviser, Dr Elizabeth Exley, University of Queensland, was extremely helpful in providing constructive comments and editorial remarks. Dr T. Woodward, University of Queensland and Dr G. Gordh, University of California, Riverside, as examiners provided corrections and advice towards publication of the thesis.

Plates 5b–d, 6a–d, 8a–c were provided by Mr J. Hardy, Electron Microscope Department, University of Queensland and Plates 2a–b, 3a, 4b–c were provided by Dr R. Raven, Queensland Museum. Sections of the male scape of *Melittobia australica* (Plates 3b–c) were cut by Mr N. Hall, Queensland Museum and photographed by Dr L. Cannon, Queensland Museum. My technician, Miss Gudrun Sarnes, was of great help checking manuscripts and numbering plates. The typists whose patience I have tried severely were Miss P. Tinniswood and Miss E. Proberts of the Queensland Museum. My wife Judith provided assistance with manuscript checking and plate assembly.

Special thanks are due to Dr J. van den Assem, University of Leiden, Holland. We have corresponded freely since 1974 and he has been of the greatest assistance with notes from his ethological studies on *Melittobia.*

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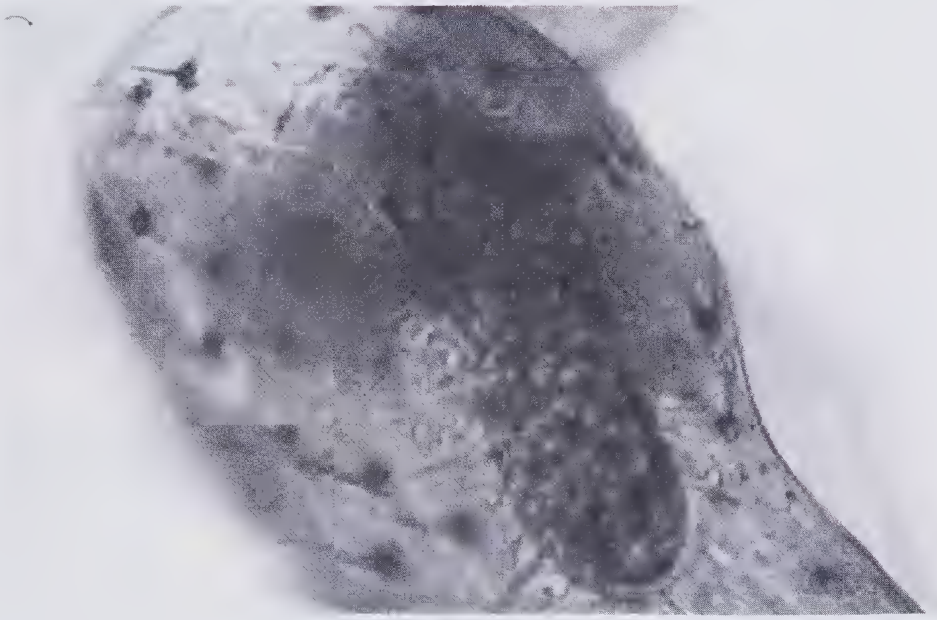
PLATE 1

Melittobia australica male scape, $AgNO_3$ stain, Euparal slide mount, × 900

a) Lateral view.
b) Ventral view.

Plate 1



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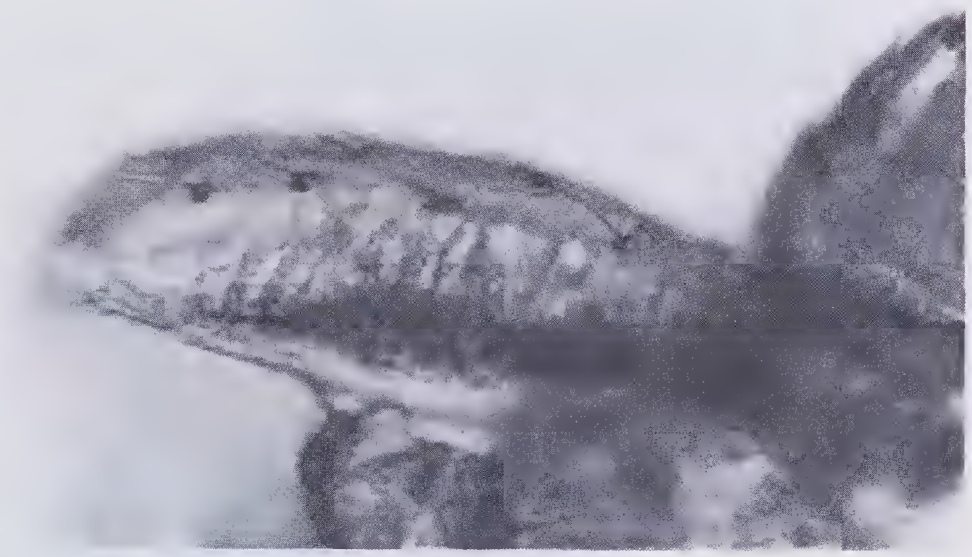


b

PLATE 2

Melittobia australica male scape.

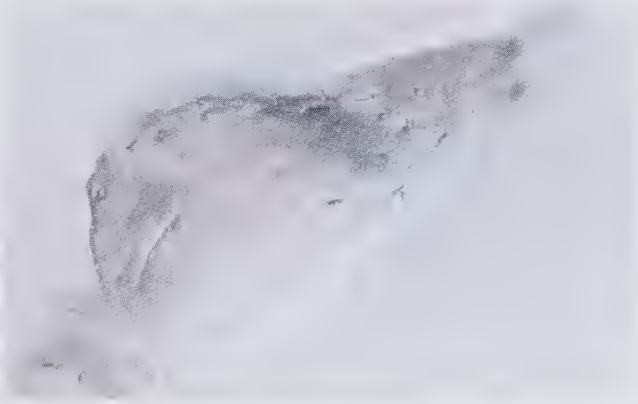
a) Dorsal view, NaOH cleared, Euparal slide mount, × 340.

b) Ventral view, showing transverse arm of gland, SEM, × 340.

c) Cuticular surface over gland, SEM, × 2,000.

Plate 2

a



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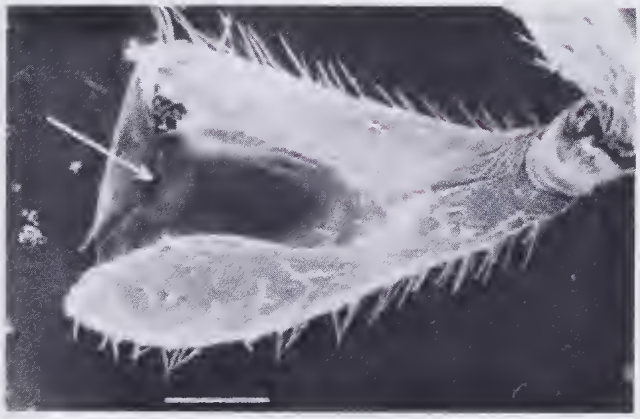
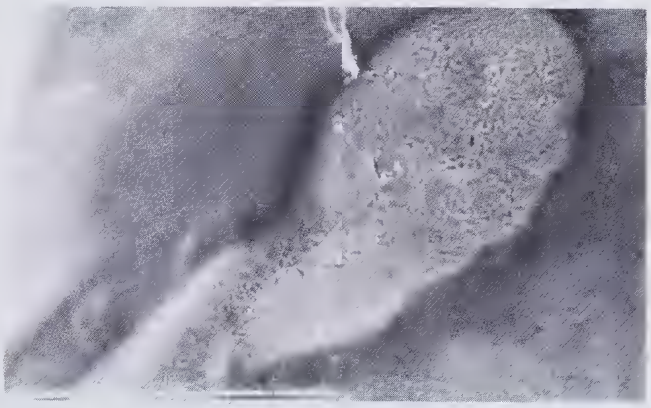




c

PLATE 3

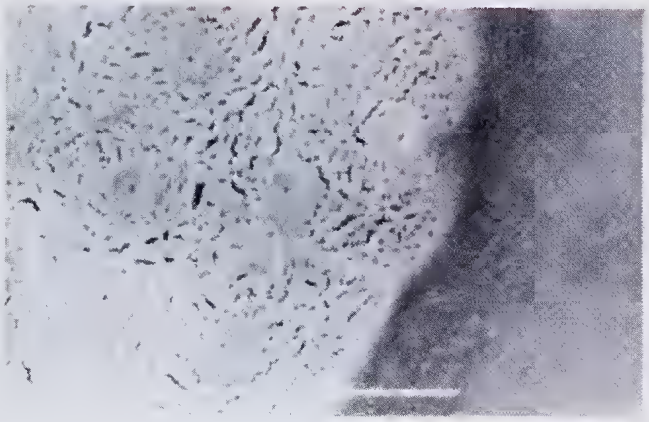
Melittobia australica male scape.

a) Cuticular surface over gland showing pores, SEM, × 5,200.

b) TS male scape just proximal of scape attachment — section through transverse arm of gland, Euparal slide mount, × 650.

c) TS more proximal region of scape-section through longitudinal area of gland, Euparal slide mount, × 700.

Plate 3



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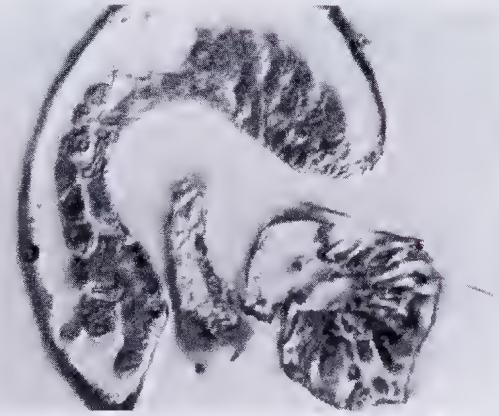
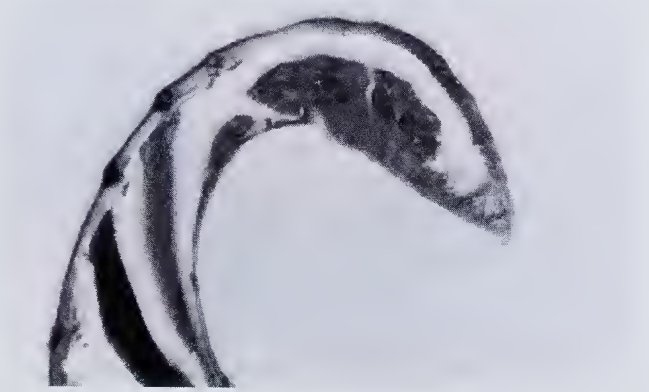




c

PLATE 4

Melittobia australica male scape and setae on legs.

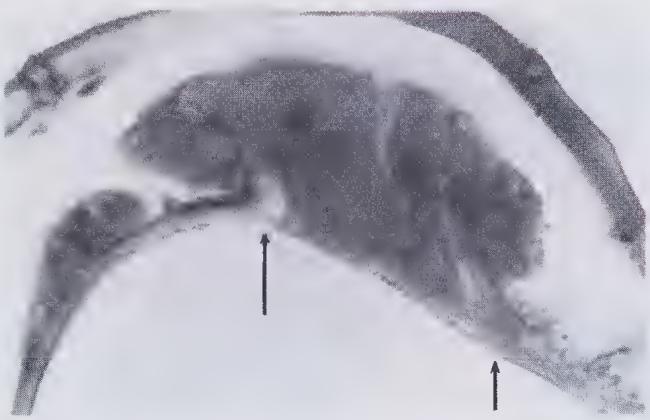
a) TS longitudinal area of scape showing cuticular invaginations to support gland, Euparal slide mount, × 2,000.

b) Dense setal tuft on ventral fore-trochanters, SEM, × 1,000.

c) Seta in mid-femoral fringe, SEM, × 4,000.

Plate 4

a



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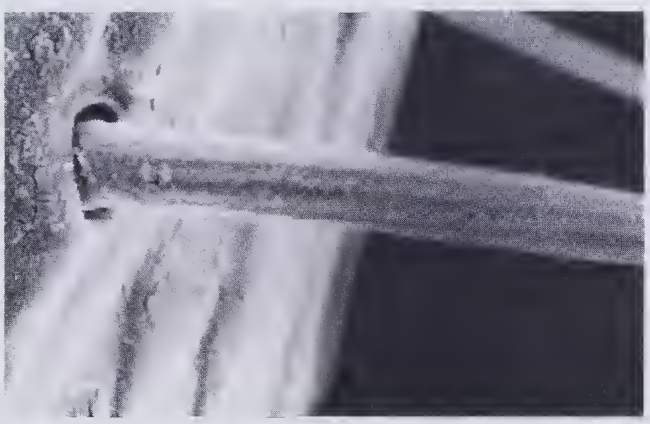


c

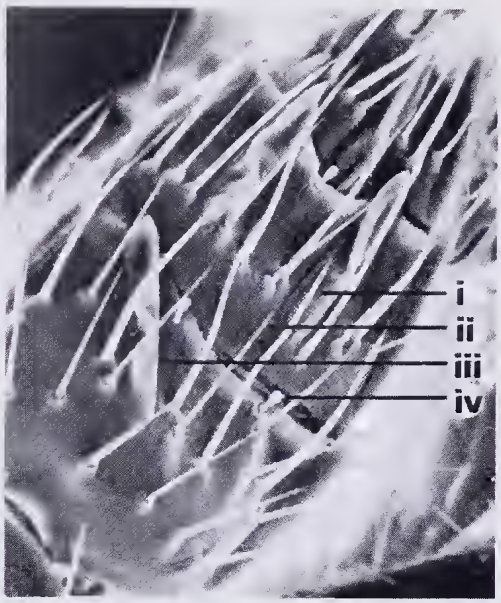
PLATE 5

Melittobia australica male, female antennae.

a) Male club, $AgNO_3$ stain, Euparal slide mount.
b) Female club, SEM, × 900.
   i) long thin unfluted setae.
   ii) tapering fluted seta.
   iii) multiporous plate sensillum.
   iv) short basiconic capitate peg.
c) Male club, segments 2 and 3, SEM, × 2,000.
d) Male tapering fluted setae, SEM, × 2,800.

Plate 5

a



b

c

d

PLATE 6

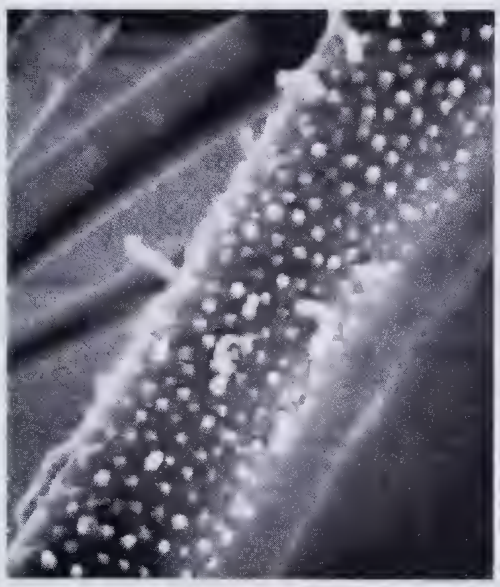
Melittobia australica male flagellum and female sensillae.

a) Male flagellum, SEM, × 600.
b) Distal female club after exposure to ethyl acetate, SEM, × 1,300.
c) Multiporous plate sensillum of freshly moulted female after exposure to ethyl acetate, SEM, × 10,000.
d) Multiporous plate sensillum of older female after exposure to ethyl acetate, SEM, × 5,500.

Plate 6

a

b



c

d

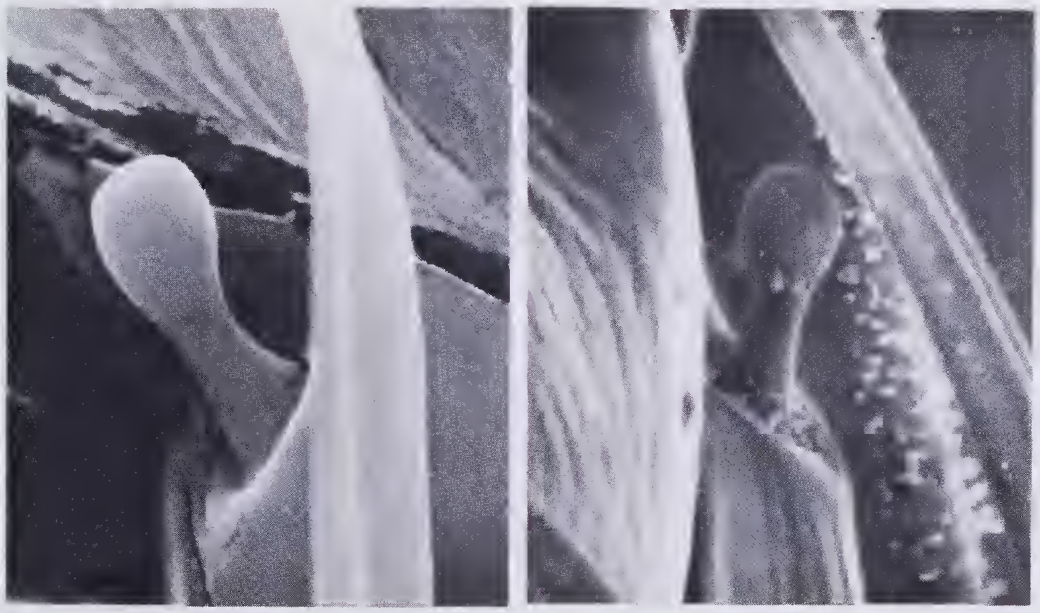
PLATE 7

Melittobia australica female short basiconic capitate pegs.

a) Older female killed by immersion in ethyl alchol, SEM, × 13,000.

b–d) Freshly moulted female after exposure to ethyl acetate, SEM, (b × 10,000; c × 18,000; d × 13,000).

Plate 7



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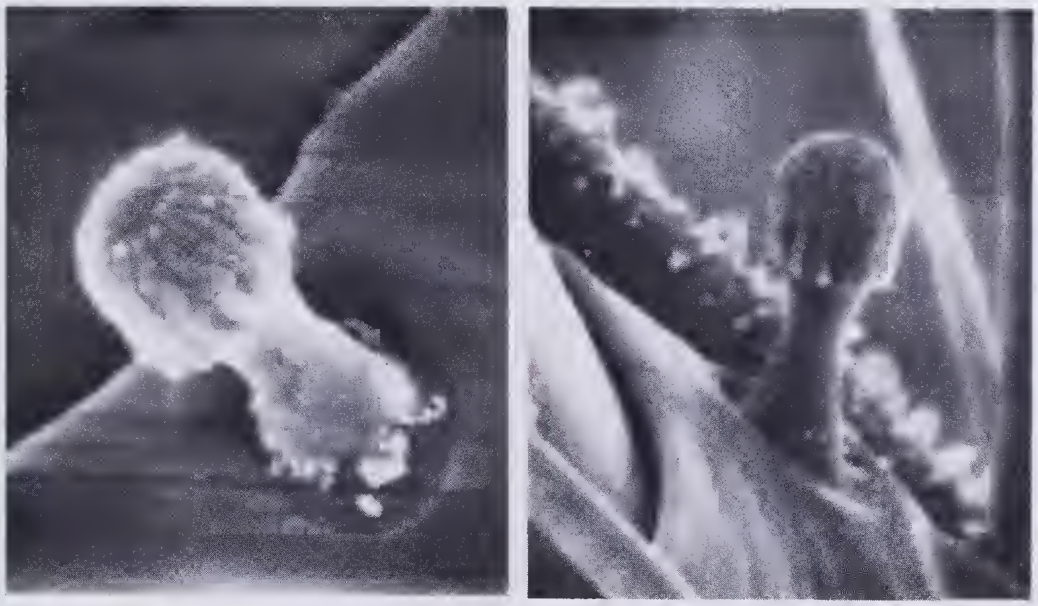


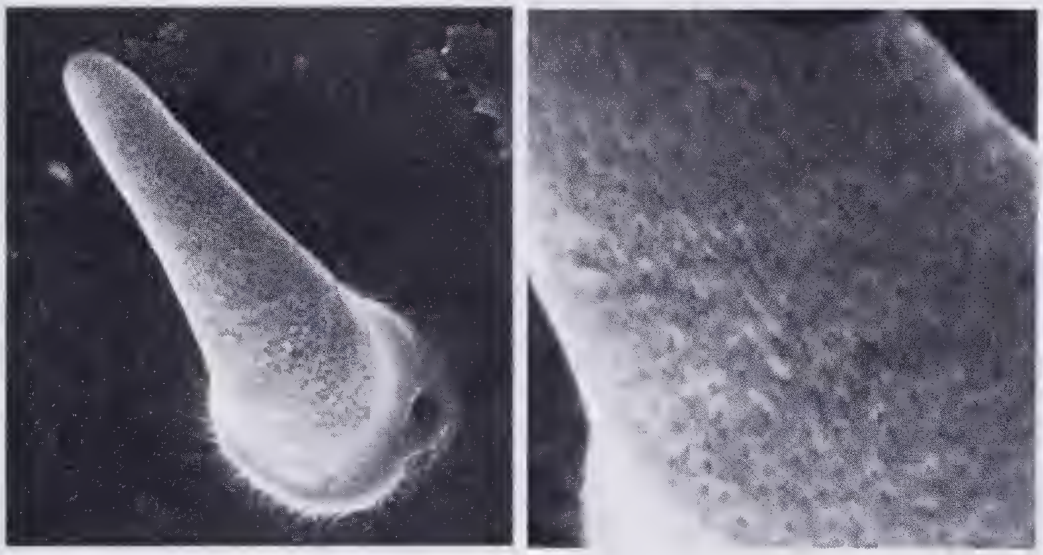
c d

PLATE 8

Grasshoper basiconic pegs.

a) Freshly moulted *Atractamorpha similis,* SEM, × 6,000.
b) Freshly moulted *Atractamorpha similis,* SEM, × 21,000.
c) Several hours after moulting *Valanga irregularis,* SEM, × 7,500.

Plate 8



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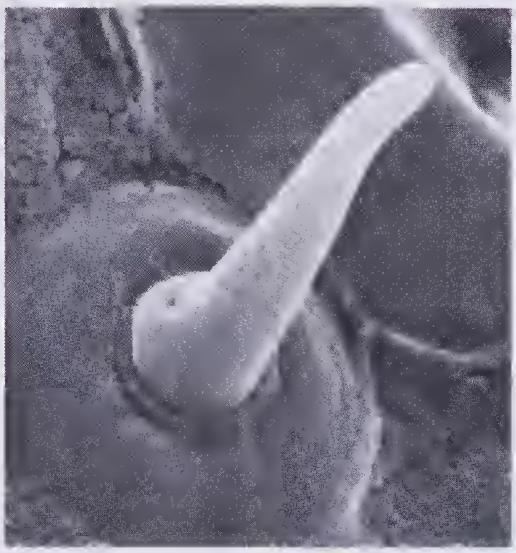

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